Marine Environmental Research 140 (2018) 243–250

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Research gaps of coral ecology in a changing world

Juliano Morais[a], Aline P.M. Medeiros[a], Bráulio A. Santos[b,*]

[a] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil
[b] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil

ARTICLE INFO

Keywords:
Cnidaria
Human disturbance
Acidification
Climate change
Overfishing
Pollution
Tourism

ABSTRACT

Coral reefs have long inspired marine ecologists and conservationists around the world due to their ecological and socioeconomic importance. Much knowledge on the anthropogenic impacts on coral species has been accumulated, but relevant research gaps on coral ecology remain underappreciated in human-modified seascapes. In this review we assessed 110 studies on coral responses to five major human disturbances– acidification, climate change, overfishing, pollution and non-regulated tourism –to identify geographic and theoretical gaps in coral ecology and help to guide further researches on the topic. We searched for papers in Web of Science published from 2000 to 2016 and classified them according to the ocean, ecoregion, human threat, level of biological organization, study approach, method of data collection, depth of data collected, and type of coral response. Most studies were carried out in the Indo-Pacific and Caribbean (36.3 and 31.9%, respectively) and used observational approach (60%) with scuba diving (36.3%) to assess the impact of ocean warming (55.4%) on coral communities (58.2%). Only 37 of the 141 global ecoregions that contain coral reefs were studied. All studies were restricted to shallow waters (0.5–27 m depth) and reported negative responses of corals to human disturbance. Our results reinforce the notion that corals are sensitive to anthropogenic changes. They reveal the scarcity of information on coral responses to pollution, tourism, overfishing and acidification, particularly in mesophotic ecosystems (> 30 m depth) and in ecoregions outside the Indo-Pacific and Caribbean. Experimental studies at the individual and population levels should be also encouraged.

1. Introduction

Coral reefs are the most diverse marine ecosystems and one of the oldest structures on Earth constituted by living organisms (Budd and Pandolfi, 2010; Carpenter et al., 2008). They provide ecosystem services like fishing, tourism, coastal protection, structural materials, and biochemicals, being vital for human societies and industries (Souter and Lindén, 2000). Despite their ecological and socioeconomic importance, they have been subjected to anthropogenic changes at varying type, intensity and frequency. Many studies have shown that global warming, ocean acidification, overfishing, pollution and non-regulated tourism are the main threats to coral reefs (McLeod et al., 2013). Combined, these human threats have significant impacts on coral abundance and distribution, affecting biodiversity from local to global scale and jeopardizing people who directly depend on coral reefs to live (Cinner et al., 2016; Edmunds, 2017; Hansen et al., 2008).

There are innumerous studies assessing different aspects of coral physiology and ecology in face of human disturbance, including several valuable reviews (Hoegh-Guldberg et al., 2007; Baker et al., 2008; Hoegh-Guldberg et al., 2017). In this review we spatialize the more recent information on the topic (2000–2016) to identify geographic and theoretical gaps and thus help to guide further research on the topic. We gathered information from Web of Science platform using the following keywords in the title: Coral reef* acidification, Coral reef* climate change, Coral reef* overfishing, Coral reef* pollution, Coral reef* tourism. This procedure resulted in 180 papers, but 70 were focused on taxonomic groups other than corals, such as fishes and algae. We excluded them and carefully analyzed the other 110 studies according to the ocean, ecoregion, human threat (i.e. acidification, climate change, overfishing, pollution, tourism), level of biological organization (i.e. individual, population, community, ecosystem level), study approach (i.e. observational or experimental), method of data collection (i.e. scuba diving, snorkel, satellite imagery, secondary data etc.), depth of data collected, and type of coral response (if positive, neutral or negative relative to the threat) (Appendix S1).

The review is structured in three sections. First, we briefly summarize the empirical evidence on the mechanisms underlying coral responses to the threats, including publications that came out before

* Corresponding author.
E-mail address: braulio@dse.ufpb.br (B.A. Santos).

https://doi.org/10.1016/j.marenvres.2018.06.021
Received 15 May 2018; Received in revised form 21 June 2018; Accepted 28 June 2018
Available online 30 June 2018
0141-1136/ © 2018 Elsevier Ltd. All rights reserved.

Table 1
Definition of the five major threats affecting corals.

Threat	Definition	Adapted from
Acidification	The predictable outcome of increased atmospheric CO_2 resulting from anthropogenic activity. As the amount of CO_2 absorbed by the oceans increases, the concentration of hydrogen ions increases, thus decreasing seawater pH.	Doney et al. (2009)
Ocean warming	A global phenomenon in which the ocean absorbs vast quantities of heat as a result of increased concentrations of greenhouse gases in the atmosphere, leading to rising ocean temperatures.	IPCC (2007)
Overfishing	Overexploitation of fish stocks below minimum levels required for species persistence and fishery economic viability. It usually results in strong cascade effects in marine ecosystems.	Jackson et al. (2001) Pauly (1988)
Pollution	The introduction by man, directly or indirectly, of substances or energy into the marine environment, including estuaries, which results or is likely to result in such deleterious effects as harm to living resources and marine life, hazards to human health, hindrance to marine activities, including fishing and other legitimate uses of the sea, impairment of quality for use of sea water and reduction of amenities	United Nations Convention on the Law of the Sea (1982), in Williams (1997)
Tourism	Comprises the activities of people traveling to and staying in places outside their usual environment for not more than one consecutive year for leisure, business and other purposes not related to the exercise of an activity remunerated from within the place visited.	Uyarra et al. (2009) O'Gorman (2009)

2000. Second, we used the outcome of our analyses to point out the current geographical and theoretical gaps in the field. Finally, we suggest further directions for filling up the gaps and guide future applied and basic research in increasingly common human-modified seascapes.

2. Threats

2.1. Ocean acidification

Large-scale human activity has caused increased CO_2 emissions, thus increasing ocean acidification levels (Feely et al., 2004). This dissolved carbon reduces seawater pH and alters its chemical components (Doney et al., 2012). About 25% of all CO_2 released into the atmosphere by anthropogenic activities annually are absorbed by the oceans (Quéré et al., 2009; Sabine et al., 2004). Basically, the increase of the CO_2 emission in the atmosphere leads to the increase of the ions of CO_2 (aqueous), HCO_3^- and hydrogen ions (H^+), and decreases CO_3^{-2} (McLeod et al., 2013). The decline in CO_3^{-2} concentration reduces the saturation state of seawater aragonite (Ωa), causing lower rates of calcification in reef-building corals (Table 1). Aragonite is the mineral form of calcium carbonate ($CaCO_3$) deposited by corals (Andersson et al., 2009; Clements et al., 2017).

Acidification is considered a global impact, but nutrient and sediment loading, which occurs locally, with fertilizer-rich sewage from plantations, may influence acidification in reefs close to urban centers (Kelly et al., 2011). The increase in CO_2 following the pre-industrial period reduced calcification and coral growth by approximately 40% by inhibiting aragonite formation (Kleypas and Langdon, 2006). During the last century, the increase in CO_2 emissions induced a reduction of the oceanic pH by ~0.1 units, from ~8.25 to ~8.14 (Orr et al., 2005). Projections suggest a decrease of 0.3 pH units by the end of the century (Caldeira and Wickett, 2003). The concentration of atmospheric carbon dioxide is expected to exceed 500 parts per million by 2050, significantly exceeding the concentration of the last 420,000 years during which most of the existing marine organisms evolved (Hoegh-Guldberg et al., 2007). These changes are likely to outweigh the ability of most organisms to adapt. By the end of the century, a few tropical corals will persist, but their functions as precipitator of calcium carbonate and coastal protector will reduce (Comeau et al., 2015; Ferrario et al., 2014).

For reef-building corals, the low levels of saturation of aragonite generates a high energy cost of calcification, which ends up harming the growth and the construction of reef structure (Doney et al., 2009). Several studies show that not only coral, but all reef-building organisms suffer damage from acidification (Kroeker et al., 2010). For example, Vogel et al. (2015) show that the coral *Acropora millepora* and the algae *Halimeda opuntia* were negatively affected by the increase in acidification and that the decrease in light availability could have an additional impact on both organisms. Using a metabolic approach, Sogin et al. (2016) demonstrate that under stressful conditions caused by acidification and rising temperatures, coral changes the pathways involved in carbohydrate metabolism, cellular structural maintenance and cell signaling. In addition, they strengthen defense mechanisms to maintain cellular activity necessary for survival at the expense of reproduction and growth. In the long run, the main consequences of ocean acidification for coral reefs are reduced survival, growth, and reproduction (Kroeker et al., 2010).

2.2. Ocean warming

The increase in the concentration of greenhouse gases is the main driver of increase in atmospheric temperature and, consequently, ocean warming (Table 1) (Wilkinson, 2008). The projected increase in sea surface temperature (SST) by the middle of the century, even from an optimistic perspective of reductions in greenhouse gas emissions, can range from 0.5 to 1.5 °C (Kirtman et al., 2013), and from 0.7 to 2.5 °C by the end of the century (Collins et al., 2013). SST has increased by 0.08 °C every decade during 1950 until 2011 (Lough, 2012), constraining the distribution of reef ecosystems (Deser et al., 2010; Kleypas et al., 1999) because many organisms are limited in their occurrence to certain thermal conditions (Drinkwater et al., 2010).

The main consequences of ocean warming on corals are major bleaching events of mass mortality (Ainsworth et al., 2016). Most of the pigmentation within corals are composed of symbiotic interactions from zooxanthellae (*Symbiodinium* spp.). The term coral bleaching refers to the partial or total loss of zooxanthellae algae (Lough and Oppen, 2009). Iglesias-Prieto et al. (1992) show that endosymbionts *Symbiodinium* start to abandon the coral when exposed to 30 °C and leave it completely at 34–36 °C. Hughes et al. (2018a) in a recent study on the Great Barrier Reef showed a strong relationship between the temperature increase and the level of bleaching in corals. This process increases respiratory rates and susceptibility to diseases that can lead to death (Kaczmarsky, 2006).

Corals live close to their thermal limits, even low changes of 1 °C or 2 °C elevation can result in large scale bleaching (Coles and Jokiel, 1978; Crabbe, 2008). As a consequence, most disease events are identified during or after bleaching (Cantin and Lough, 2014), although they may partially or fully recover from bleaching events (Depczynski et al., 2013). Examples of mass mortality associated with bleaching have been documented, reducing coral cover and modifying the structure and function of the entire benthic community (Buglass et al., 2015; Burt et al., 2011; Guest et al., 2016; Marimuthu et al., 2013; Swain et al., 2016; Thompson and Dolman, 2010; Wild et al., 2011). Actually, the consequences of bleaching may be classified into two broad categories: immediate and longer term effects (Baker et al., 2008).

Immediate effects involve decreased tissue and skeletal growth, increased susceptibility to disease and mortality, and negative impacts on coral reef organisms. Longer term effects involve reduced coral reproduction and recruitment, bioerosion, change in algal symbiont communities, and time lags in coral responses related to coral morphology, size, and the species involved (Baker et al., 2008).

2.3. Overfishing

Overfishing is present in almost all reefs close to human settlements (Sandin et al., 2008) and has been considered the main driver of algae dominance in reef ecosystems (Hughes et al., 2010; Jackson et al., 2001). In healthy coral reefs, herbivory by fishes is largely responsible for controlling algal accumulation (Rasher et al., 2012), leaving space for corals to thrive even under scenarios of fast algal growth (McClanahan et al., 2012). As the populations of herbivorous fishes are reduced by overfishing (Table 1), top-down control of algal biomass is lost and corals are gradually replaced by algae (Burkepile and Hay, 2006; Mumby et al., 2007). According to Ceccarelli et al. (2006), the area covered by some species of algae may increase from 20 to 50% with the total exclusion of large herbivorous fishes.

In addition to the control of algae, some fishes are also responsible for the control of sponge proliferation. In the Caribbean, in places with high overfishing, the number of sponges that were in competition with corals was double compared with places without overfishing (Loh et al., 2015). Consequently, all species that live associated with the corals have their populations negatively affected, with cascade effects on the structure and functions of the reef communities (Stella et al., 2011). In a simplistic view, we may identify four links among fishes, algae, and corals: (1) herbivorous fishes consume algae, (2) algae compete with and displace corals, (3) corals generate habitat complexity for fishes, and (4) fishes require habitat complexity for feeding, protection, nursery and reproductive sites (Mumby, 2016). Therefore, any disruption in these links can collapse the reef ecosystem. The same rationale may apply for some fish-sponge-coral interactions that involve competing sponges and corals.

2.4. Pollution

Contamination of coastal waters with residential, industrial and agricultural sewage has been a major concern in tropical countries (Byamukama et al., 2005). Some studies addressing the impacts of pollution on coral reefs indicate that the elevated content of inorganic nutrients could lead to increased algal growth and coral diseases (Fabricius et al., 2005). Others point out that areas with high levels of pollution are characterized by low local coral diversity, low coral recruitment, high mortality rates, low skeletal density, reduced depth distribution, high bioerosion rates, and shift in community dominance from hard corals to organisms that are not capable of building reefs (West and Woesik, 2001). A study conducted in French Polynesia showed widespread contamination at all sampling sites and in all species studied with herbicide derivatives and insecticides (Roche et al., 2011), indicating the potential for large-scale shifts in coral populations.

Like overfishing, pollution favors algal dominance in reef ecosystems by weakening the bottom-up regulation of algal populations, as the input of nutrients is translated into increased algal biomass (Zaneveld et al., 2016). A work on the Red Sea showed that a 50% increase in nutrients from floating fish farms caused benthic algal blooms, incremented coral mortality by about 50% and reduced calcification by 3–4 times (Loya et al., 2004). The models estimating pollution in coral reefs around the world show that 22% of all coral reefs are classified as highly threatened and 12% as average threatened (Burke et al., 2012). Pollution is also associated with deforestation and countries with high deforestation levels (Table 1), such as Taiwan and Vietnam, which half of their reefs at risk (Burke et al., 2002). In general, pollution is as important for reef conservation as bleaching and acidification, but efforts to understand this impact have been smaller (Fabricius, 2005).

2.5. Non-regulated tourism

In many tropical countries, coral reef based tourism is growing faster than any other tourism segment (Table 1), being a key component of the global tourism industry (Milazzo et al., 2002). Cesar et al. (2003) estimated that reefs generate $29.8 billion in global net benefits per year, while Richmond (1993) in the Great Barrier Reef estimated that tourism generates $1.5 billion per year for Queensland, Australia. Tourism activities directly affect the corals through physical contact with diver fins, anchors, and collision of boat bottom with corals (Dearden et al., 2007). They also affect the corals indirectly by the addition of pollutants and other toxic substances from tourists and vessels, and by increasing water turbidity (Dearden et al., 2007; Reopanichkul et al., 2009).

Evidence shows that non-regulated tourism degrades the reef and reduces its value as tourist spot, attracting fewer tourists in the long run (Hasler and Ott, 2008). About 90% of divers assume that they had physical contacts with reefs during diving, and the major causes of coral damage are the fins (45.5%), followed by hands (19.5%) and equipment (15.9%) (Barker and Roberts, 2004; Ku and Chen, 2013; Roche et al., 2016). In Akumal, Mexico, there is a clear link between snorkel-based tourism and the decline in coral cover over time and space (Gil et al., 2015), though it has been recently reverted by local regulations that allow only 360 divers per day to snorkel in a limited area (guided and without fins). Because coral degradation often leads to fish impoverishment, tourists prefer to visit more conserved coral reefs. In this sense, adjusting the quantity of visitants to the biotic features of the reef is mandatory to conciliate sustainable exploration and conservation (Uyarra et al., 2009).

3. Knowledge gaps

In this section we present the outcomes of the analyses of the 110 studies that fell into our search criteria. We divided the findings into geographic and theoretical gaps.

3.1. Geographic gaps

As expected, most studies were performed in regions where the global coral diversity is concentrated: the Indo-Pacific, with 36.3% of all studies, and the Caribbean, with 31.9% (Fig. 1). Only 37 of the 141 global ecoregions that contain coral reefs (Veron et al., 2009) have been studied. Three ecoregions had more than five studies: two in the Tropical Northwestern Atlantic (The Greater Antilles and Western Caribbean) and one in the Northeast Australian Shelf (Central and Southern Great Barrier Reef). This not only corroborates the general perception among scientists that our current knowledge on coral responses to human disturbances is biased geographically, but also demonstrates we are still unable to guide effective global actions of coral management and conservation.

The other works were distributed across the Southwestern Atlantic (3.6%), Pacific Islands (8.1%), Asia (5.4%), some seas of Africa (5.4%), and in the central part of the Indian (2.7%), plus some studies that did not mention the location (6.6%) (Fig. 1). Besides concentrating the global richness of coral species, the Indo-Pacific and the Caribbean are close to countries that have historically funded research on coral ecology. For example, in Australia we find many studies because it is a country with great investment in the science and conservation of coral reefs. The United States of America also supports coral research for decades. Other countries that host large reef formations of global relevance, such as Brazil, have poorly contributed to coral ecology.

Brazilian coral species richness is low compared with that of

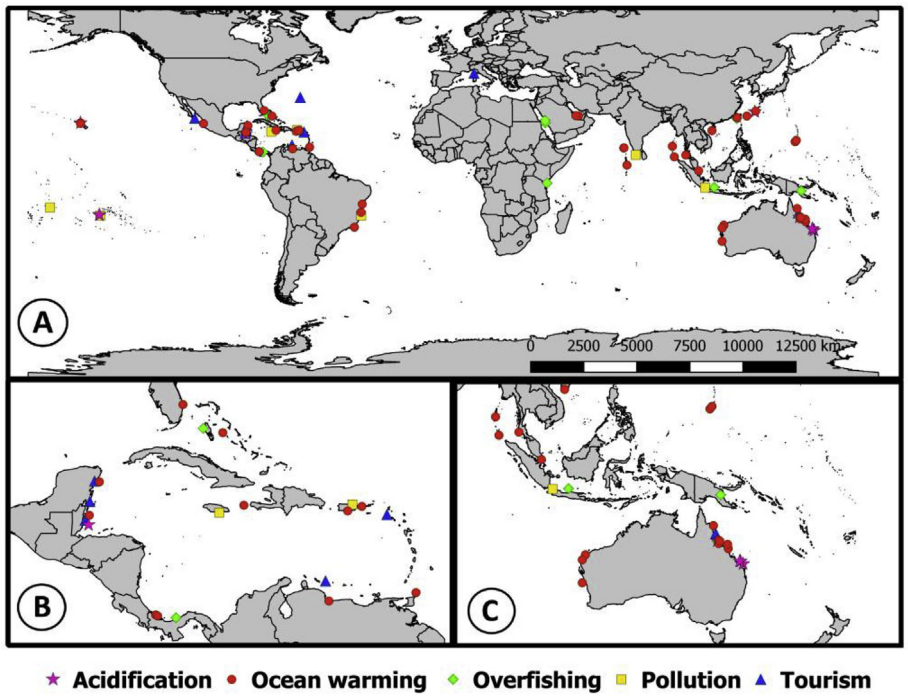

Fig. 1. Sites where studies on coral responses to anthropogenic threats were carried out. (A) Global view, (B) Caribbean region, (C) Indo-pacific region.

Caribbean reefs (Leão et al., 2016). It has fewer reef-building species, but higher levels of endemism and are predominantly composed of massive forms (Castro and Pires, 2001). Environmental conditions, such as strong solar radiation, low light levels and high sediment influx, seem to have shaped the high tolerance of most Brazilian coral species to unsuitable conditions (Leão et al., 2003; Sassi et al., 2015). Only the most adapted species tolerate the stressful conditions of the South-western Atlantic waters (Leão et al., 2016), and as such, it is possibly that they are less sensitive to human disturbances than Caribbean and Indo-Pacific species. This remains to be examined.

The Red Sea is other important geographic gap of coral ecology. It hosts 346 zooxanthellated and azooxanthellated scleractinian coral species, from which 19 (5.5%) are endemic, such as *Acropora parapharaonis, Montipora aspergillus, Montipora hemispherica, Pachyseris inattesa* (Dibattista et al., 2016). About 14% of its reef fishes are endemic as well, including 7 unique species of butterfly fishes (Randall, 1998), but neither coral responses to human threats nor fish-coral interactions have been sufficiently studied.

The Persian Gulf deserves more attention too. With a low diversity but species well adapted to the harsh conditions (e.g. *Acropora downingi, Acropora clathrata* and *Porites harrisoni*), the Persian Gulf might reveal pathways towards novel coral reefs (Graham et al., 2014). Their species are able to withstand the cold temperatures of the winter and the warmer temperatures of the summer more than any other around in the world (Coles and Riegl, 2013). This creates an important point of study to understand coral adaptation to climate change and the effects of temperature on coral reefs (Burke et al., 2012; Coles and Riegl, 2013).

The American Samoa, where up to 85 coral species inhabiting reef-flat pools can withstand daily fluctuations of 6 °C (from 28 °C to 34 °C), should be more studied as well (Craig et al., 2001). During the 17 years following this paper, researches on molecular genetics, physiology and resilience have been conducted comparing corals in the stressful reef flat pools to those in the benign open ocean reef front (e.g., Smith and Birkeland, 2007; Gold and Palumbi, 2018). The main goal of this long-term research program has been to develop “designer reefs”, i.e., coral reef communities composed of genetic stock that had shown resilience in the harsh environments of the reef-flat pools. It has helped to identify the mechanisms underlying coral resistance to climate change and to improve models of coral demise under warmer conditions (Palumbi et al., 2014). This inspiring successful initiative should be replicated in poorly studied regions.

3.2. Theoretical gaps

More than half of the studies focused on ocean warming (55.4%), which could be directly linked with climate change and its direct influence in SST increasing. Combined, ocean acidification (13.6%), tourism (10.9%), overfishing (10%), and pollution (9.1%) accounted for less than half of the studies (Fig. 2). This demonstrates that current conclusions on how corals respond to anthropogenic alterations are biased towards only one human threat (i.e. ocean warming). In addition, even this most-studied threat is scantly understood if we consider the global distribution of coral reefs (Crabbe, 2008). In practical terms, this finding suggests we are not totally prepared to support decision-makers to protect coral against the major human threats, even in the most studied sites.

In terms of biological organization, most studies focused on the community level (58.2%) taking into consideration different aspects of species composition and diversity, 25.5% were conducted at the ecosystem level and a few addressed issues at the individual (7.3%) or population levels (9.1%) (Fig. 2). It is well known that populations and individuals may respond differently to changes in the environment (Edmunds et al., 2016). Some populations may disappear following disturbance while others may thrive, determining species response to disturbance. Because different species may have different functions in the reef ecosystem (Clements, 2000), this knowledge gap results in uncertainty about how coral diversity may be maintained in human-modified seascapes.

Almost 60% of the studies were observational, 23.6% were experimental, and 16.4% gathered data from the literature (Fig. 2). Experimental studies are critical to isolate variables, manipulate conditions and simulate future scenarios of environmental alterations. They should be more common in the literature. Observational studies are critical as well. Their findings are useful to describe patterns at several spatial and temporal scales and to infer potential processes underlying the patterns

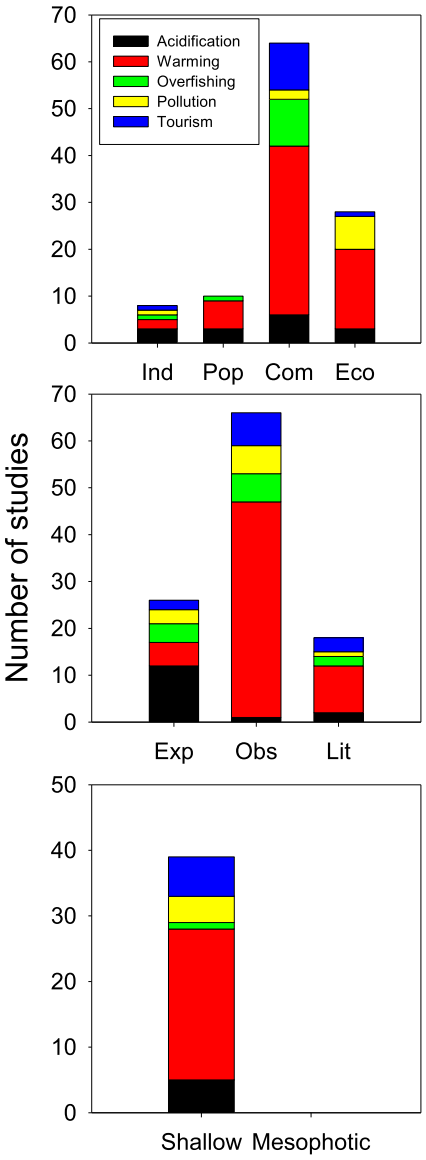

Fig. 2. Number of studies per human threat according to the level of biological organization [individual (ind), population (pop), community (com), ecosystem (eco)], study approach [experimental (exp), observational (obs), literature (lit)] and depth [shallow (up to 30 m), mesophotic (30–150 m)]. N = 110 studies.

(Sasano et al., 2016), but the validation of cause-and-effect relationships usually require an experimental approach. The ideal study should include approaches to combine the correlative evidence derived from observational approach with the cause-and-effect evidence derived from manipulation (Bartlett, 2013). Such manipulation is more indicative of individual- or population-level studies (Bongaerts et al., 2017), but communities may be also artificially structured and designed to answer specific questions (Edmunds et al., 2016).

Despite the ocean, ecoregion, depth, level of biological organization, and methods used, 100% of the studies reported negative responses of corals to the five threats considered. Such sensitivity is not novel, but 100% of negative responses was quite surprising as some coral species are supposed to overcome the harsh conditions (Coles and Riegl, 2013). The most reported negative responses were bleaching (27.2%), mortality (13.6%), and reduced calcification (10.9%), but disease, intoxication, physical damage, reduced coverage, immune response and metabolic loss were also reported. This finding reinforces the notion that corals are vulnerable to anthropogenic changes (Edmunds et al., 2014; Freeman et al., 2013; Hoegh-Guldberg et al., 2017).

Another important gap was the absence of studies below 30 m depth (Fig. 2), revealing that there is no work so far explicitly designed to examine how mesophotic corals respond to human disturbances. Since the deep reef refugia hypothesis was postulated about two decades ago (Glynn, 1996), many studies have been developed to describe several aspects of coral biology along the gradient of depth (Bongaerts et al., 2010; Loya et al., 2016; Morais and Santos, 2018; Shlesinger et al., 2017). Studies comparing mesophotic reefs with contrasting levels of human disturbance or monitoring the same mesophotic reef following different anthropogenic impacts are lacking yet. Without this information, it is hard to estimate the potential of deep corals to replenish not only human-disturbed shallow reefs, as the hypothesis predicts, but also other deep reefs impacted by humans (Kahng and Grigg, 2005).

One of the explanations for the lack of studies in mesophotic reefs is the logistic and methodological requirements involved in data collection (Hinderstein et al., 2010; Kahng et al., 2010). In recent years, technology has helped researchers to estimate the abundance and distribution of deep coral species (Kahng et al., 2014), as going below the 40 m requires tech divers (with open scuba circuits) or fully closed circuit electronic rebreathers. Remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) have been replacing divers and are promising, but their elevated cost usually makes the research unfeasible (Menza et al., 2007; Wynn et al., 2014). This might explain why we found no work using such vehicles in data collection. In fact, most studies collected their data with recreational scuba divers (36.3%) at shallow depths (up to 27 m); the other studies adopted a myriad of methodological procedures, from snorkel and interviews to satellite images, fossil records, and secondary data.

4. Future directions

Although we have not included papers published before 2000 and scientific journals not indexed to the Web of Science, we suggest five directions for future research on coral ecology in human-modified seascapes. First, giving more attention to regions outside the Indo-Pacific and the Caribbean, because many places with relevant importance for global coral diversity are undersampled. For example, the corals of the Southwestern Atlantic with its high level of endemism (Leão et al., 2016), and the corals of the Persian Gulf with their capacity of supporting remarkable amplitude of variation in temperature (Coles and Riegl, 2013), have been scantly studied. The Southwestern Atlantic does not even appear in a recent global assessment of mass bleaching (Hughes et al., 2018b).

Second, more efforts should be applied to assess the effects of acidification, overfishing, pollution, and non-regulated tourism on coral growth, mortality, reproduction, dispersal, abundance and distribution. These issues have been studied for many decades (e.g. Jackson et al., 2001; Johannes, 1975), but our findings indicate that they have received less attention than ocean warming between 2000 and 2016. There is much to be documented on the outcome of SST on corals as well (Hughes et al., 2018a; b), but these less studied threats deserve the same attention.

Third, it is needed to intensify coral research in mesophotic zones (Esser et al., 2010), identifying depth-specialists and depth-generalists species and assessing the role of deep reef to serve as refuges for corals (Bongaerts et al., 2010). The depth-generalists, i.e., those species occurring in shallow and deep waters, are particularly important for the recovery of more disturbed shallow reefs and should be examined from genetic and ecological perspectives (Bongaerts et al., 2017; Morais and Santos, 2018). Fourth and linked to that is the developing of more cost-effective technology for assessing deep waters (e.g. cheaper ROVs, AUVs, and rebreathers) and for remote sensing of tourism, fishing and polluting activities (Sasano et al., 2016; Scopelitis et al., 2009). These technologies should be available for researchers in both developing and developed countries.

Finally, we suggest more experimental studies to uncover between-individual and between-population differences along gradients of human disturbance, and if possible, decoupling the response into genetic and environmental components. This will possibly help to identify the 'winner' species, i.e. those that are more likely to benefit from the anthropogenic changes in seascapes. By identifying these species, we may forecast the taxonomic and functional composition of the future coral community, and shed light into the functioning of the novel coral reefs (Fabricius et al., 2011; Graham et al., 2014). Given the biogeographic history of the oceans (Spalding et al., 2007; Veron et al., 2009), this procedure should not be concentrated in particular regions, but well distributed across the coral reefs of the globe.

More importantly, we should be fast and skillful enough to translate the scientific knowledge into conservation actions soon. Estimates indicate we have functionally lost at least 25% of the world's coral reefs, and a third of all coral species are threatened with extinction (Carpenter et al., 2008). From 1969 to 2011, living coral cover on Caribbean reefs declined about 41% with reefs between 15° and 25°N steeply dropping from 35% to 16%, while reefs north and south of those latitudes remaining relatively stable (Jackson et al., 2014). These changes have been mainly driven by the threats considered here, plus low legal protection of marine and coastal ecosystems, management failures, urbanization, port development and other human activities that jeopardize marine biodiversity (Sarkar and Ghosh, 2013). We expect that the geographic and theoretical gaps summarized in this review help to boost coral research and ultimately influence decision-making involved in coral reef management and conservation.

Acknowledgments

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) and Fundação de Apoio à Pesquisa do Estado da Paraíba (Fapesq-PB) for the graduate scholarships provided to JM and APMM, respectively. The Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number 310340/2016-0), Fundação Grupo Boticário de Proteção à Natureza (grant number 1044-20152) and Padi Foundation (application number 32777) provided financial support. We are grateful to an anonymous reviewer for critical comments on previous version of this manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.06.021.

References

Ainsworth, T.D., Heron, S.F., Ortiz, J.C., Mumby, P.J., Grech, A., Ogawa, D., Eakin, C.M., Leggat, W., 2016. Climate change disables coral bleaching protection on the Great Barrier Reef. Science 352, 338–342. http://dx.doi.org/10.1017/CBO9781107415324.004.

Andersson, A.J., Kuffner, I.B., Mackenzie, F.T., Jokiel, P.L., Rodgers, K.S., Tan, A., 2009. Net Loss of $CaCO_3$ from a subtropical calcifying community due to seawater acidification: mesocosm-scale experimental evidence. Biogeosciences 6, 1811–1823.

Baker, A.C., Glynn, P.W., Riegl, B., 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar. Coast Shelf Sci. 80, 435–471. http://dx.doi.org/10.1016/j.ecss.2008.09.003.

Barker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biol. Conserv. 120, 481–489. http://dx.doi.org/10.1016/j.biocon.2004.03.021.

Bartlett, T.C., 2013. Small Scale Experimental Systems for Coral Research: Considerations, Planning, and Recommendations. NOAA Technical Memorandum NOS NCCOS 165 and CRCP 18. 68pp. .

Bongaerts, P., Ridgway, T., Sampayo, E.M., Hoegh-Guldberg, O., 2010. Assessing the "deep reef refugia" hypothesis: focus on Caribbean reefs. Coral Reefs 29, 309–327. http://dx.doi.org/10.1007/s00338-009-0581-x.

Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S.R., Hoegh-Guldberg, O., 2017. Deep reefs are not universal refuges: reseeding potential varies among coral species. Sci. Adv 3, e1602373. http://dx.doi.org/10.1126/sciadv.1602373.

Budd, A.F., Pandolfi, J.M., 2010. Evolutionary novelty is concentrated at the edge of coral species distributions. Science 328, 1558–1561. http://dx.doi.org/10.1126/science.1188947.

Buglass, S., Donner, S.D., Alemu, I., J, B., 2015. A study on the recovery of Tobago's coral reefs following the 2010 mass bleaching event. Mar. Pollut. Bull. 104, 198–206. http://dx.doi.org/10.1016/j.marpolbul.2016.01.038.

Burke, L., Selig, E., Spalding, M., 2002. Reefs at Risk in Southeast Asia. World Resour. Institute, Washington,DC.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2012. Reefs at Risk Revisited. World Resour. Institute, Washington,DC.

Burkepile, D.E., Hay, M.E., 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87, 3128–3139. http://dx.doi.org/10.1890/0012-9658(2006)87[3128:HVNCOM]2.0.CO;2.

Burt, J., Al-Harthi, S., Al-Cibahy, A., 2011. Long-term impacts of coral bleaching events on the world's warmest reefs. Mar. Environ. Res. 72, 225–229. http://dx.doi.org/10.1016/j.marenvres.2011.08.005.

Byamukama, D., Mach, R.L., Kansiime, F., Manafi, M., Farnleitner, A.H., 2005. Discrimination efficacy of fecal pollution detection in different aquatic habitats of a high-altitude tropical country, using presumptive coliforms, *Escherichia coli*, and *Clostridium perfringens* spores. Appl. Environ. Microbiol. 71, 65–71. http://dx.doi.org/10.1128/AEM.71.1.65.

Caldeira, K., Wickett, M.E., 2003. Anthropogenic carbon and ocean pH. Nature 425, 365. http://dx.doi.org/10.1038/425365a.

Cantin, N.E., Lough, J.M., 2014. Surviving coral bleaching events: Porites growth anomalies on the great barrier reef. PLoS One 9 (2), e88720. http://dx.doi.org/10.1371/journal.pone.0088720.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortes, J., Delbeek, J.C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzman, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C., Weil, E., Wood, E., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321, 560–563. http://dx.doi.org/10.1126/science.1159196.

Castro, C.B., Pires, D.O., 2001. Brazilian coral reefs: what we already know and what is still missing. Bull. Mar. Sci. 69, 357–371.

Ceccarelli, D.M., Hughes, T.P., Mccook, L.J., 2006. Impacts of simulated overfishing on the territoriality of coral reef damselfish. Mar. Ecol. Prog. Ser. 309, 255–262. http://dx.doi.org/10.3354/meps309255.

Cesar, H., Burke, L., Pet-Soede, L., 2003. The Economics of Worldwide Coral Reef Degradation. Cesar Environmental Economics Consulting (CEEC), Arnhem, pp. 23.

Cinner, J.E., Pratchett, M.S., Graham, N.A.J., Messmer, V., Fuentes, M.M.P.B., Ainsworth, T., Ban, N., Bay, L.K., Blythe, J., Dissard, D., Dunn, S., Evans, L., Fabinyi, M., Fidelman, P., Figueiredo, J., Frisch, A.J., Fulton, C.J., Hicks, C.C., Lukoschek, V., Mallela, J., Moya, A., Penin, L., Rummer, J.L., Walker, S., Williamson, D.H., 2016. A framework for understanding climate change impacts on coral reef social-ecological systems. Reg. Environ. Change 16, 1133–1146. http://dx.doi.org/10.1007/s10113-015-0832-z.

Clements, W.H., 2000. Integrating effects of contaminants across levels of biological organization: an overview. J. Aquatic Ecosyst. Stress Recovery 7, 113–116. http://dx.doi.org/10.1023/A:1009927612391.

Clements, J.C., Bourque, D., Mclaughlin, J., Stephenson, M., Comeau, L.A., 2017. Extreme ocean acidification reduces the susceptibility of eastern oyster shells to a polydorid parasite. J. Fish. Dis. 40, 1573–1585. http://dx.doi.org/10.1111/jfd.12626.

Coles, S.L., Jokiel, P.L., 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. Mar. Biol. 49, 187–195.

Coles, S.L., Riegl, B.M., 2013. Thermal tolerances of reef corals in the Gulf: a review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. Mar. Pollut. Bull. 72, 323–332. http://dx.doi.org/10.1016/j.marpolbul.2012.09.006.

Collins, M., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, Pierre, Gao Jr., X., G, W.J., Johns, T., Krinner, Gerhard, Shongwe, M., Tebaldi, C., Weaver, A.J., Wehner, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. http://dx.doi.org/10.1017/CBO9781107415324.024.

Comeau, S., Carpenter, R.C., Lantz, C.A., Edmunds, P.J., 2015. Ocean acidification accelerates dissolution of experimental coral reef communities. Biogeosciences 12, 365–372. http://dx.doi.org/10.5194/bg-12-365-2015.

Crabbe, M.J.C., 2008. Climate change, global warming and coral reefs: modelling the effects of temperature. Comput. Biol. Chem. 32, 311–314. http://dx.doi.org/10.1016/j.compbiolchem.2008.04.001.

Craig, P., Birkeland, C., Belliveau, S., 2001. High temperatures tolerated by a diverse assemblage of shallow-water corals in American Samoa. Coral Reefs 20, 185–189.

Dearden, P., Bennett, M., Rollins, R., 2007. Perceptions of diving impacts and implications for reef conservation perceptions of diving impacts and implications. Coast. Manag. 35, 305–317. http://dx.doi.org/10.1080/08920750601169584.

Depczynski, M., Gilmour, J.P., Ridgway, T., Barnes, H., Heyward, A.J., Holmes, T.H., Moore, J.A.Y., Radford, B.T., Thomson, D.P., Tinkler, P., Wilson, S.K., 2013. Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. Coral Reefs 32, 233–238. http://dx.doi.org/10.1007/s00338-012-0974-0.

Deser, C., Alexander, M.A., Xie, S., Phillips, A.S., 2010. Sea surface temperature variability : patterns and mechanisms. Ann. Rev. Mar. Sci. 2, 115–143. http://dx.doi.org/10.1146/annurev-marine-120408-151453.

Dibattista, J.D., Roberts, M.B., Bouwmeester, J., Bowen, B.W., Coker, D.J., Lozano-Cortés, D.F., Howard Choat, J., Gaither, M.R., Hobbs, J.P.A., Khalil, M.T., Kochzius, M.,

Myers, R.F., Paulay, G., Robitzch, V.S.N., Saenz-Agudelo, P., Salas, E., Sinclair-Taylor, T.H., Toonen, R.J., Westneat, M.W., Williams, S.T., Berumen, M.L., 2016. A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. J. Biogeogr. 43, 423–439. http://dx.doi.org/10.1111/jbi.12649.

Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean acidification: the other CO_2 problem. Ann. Rev. Mar. Sci. 1, 169–194. http://dx.doi.org/10.1146/annurev.marine.010908.163834.

Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. Annu. Rev. Ecol. Evol. Syst. 4, 11–37. http://dx.doi.org/10.1146/annurev-marine-041911-111611.

Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H., Polovina, J.J., Takasuka, A., 2010. On the processes linking climate to ecosystem changes. J. Mar. Syst. 79, 374–388. http://dx.doi.org/10.1016/j.jmarsys.2008.12.014.

Edmunds, P.J., 2017. Intraspecific variation in growth rate is a poor predictor of fitness for reef corals. Ecology 38, 42–49. http://dx.doi.org/10.1111/ijlh.12426.

Edmunds, P.J., Adjeroud, M., Baskett, M.L., Baums, I.B., Budd, A.F., Carpenter, R.C., Fabina, N.S., Fan, T.Y., Franklin, E.C., Gross, K., Han, X., Jacobson, L., Klaus, J.S., McClanahan, T.R., O'Leary, J.K., Van Oppen, M.J.H., Pochon, X., Putnam, H.M., Smith, T.B., Stat, M., Sweatman, H., Van Woesik, R., Gates, R.D., 2014. Persistence and change in community composition of reef corals through present, past, and future climates. PLoS One 9 (10), e107525. http://dx.doi.org/10.1371/journal.pone.0107525.

Edmunds, P.J., Comeau, S., Lantz, C., Andersson, A., Briggs, C., Cohen, A., Gattuso, J.-P., Grady, J.M., Gross, K., Johnson, M., Muller, E.B., Ries, J.B., Tambutté, S., Tambutté, E., Venn, A., Carpenter, R.C., 2016. Integrating the effects of ocean acidification across functional scales on tropical coral reefs. Bioscience 66, 350–362. http://dx.doi.org/10.1093/biosci/biw023.

Esser, M.P., Lattery, M., Stat, M., Ojimi, M., Gates, R.D., Grottoli, A., 2010. Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. Ecology 91, 990–1003. http://dx.doi.org/10.1890/09-0313.1.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146. http://dx.doi.org/10.1016/j.marpolbul.2004.11.028.

Fabricius, K., Ath, G. De, Mccook, L., Turak, E., Mcb, D., 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar. Pollut. Bull. 51, 384–398. http://dx.doi.org/10.1016/j.marpolbul.2004.10.041.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S., Lough, J.M., 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nat. Clim. Change 1, 165–169. http://dx.doi.org/10.1038/nclimate1122.

Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305, 362–366.

Ferrario, F., Beck, M.W., Storlazzi, C.D., Micheli, F., Shepard, C.C., Airoldi, L., 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat. Commun. 5, 1–9. http://dx.doi.org/10.1038/ncomms4794.

Freeman, L.A., Kleypas, J.A., Miller, A.J., 2013. Coral reef habitat response to climate change scenarios. PLoS One 8, 1–14. http://dx.doi.org/10.1371/journal.pone.0082404.

Gil, M.A., Renfro, B., Figueroa-Zavala, B., Penié, I., Dunton, K.H., 2015. Rapid tourism growth and declining coral reefs in Akumal, Mexico. Mar. Biol. 162, 2225–2233. http://dx.doi.org/10.1007/s00227-015-2748-z.

Glynn, P. w, 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biol. 2, 495–509. http://dx.doi.org/10.1111/j.1365-2486.1996.tb00063.x.

Gold, Z., Palumbi, S.R., 2018. Long-term growth rates and effects of bleaching in Acropora hyacinthus. Coral Reefs 37, 267–277. https://doi.org/10.1007/s0033.

Graham, N.A.J., Cinner, J.E., Norstrom, A.V., Nystrom, M., 2014. Coral reefs as novel ecosystems: embracing new futures. Curr. Opin. Environ. Sust. 7, 9–14. http://dx.doi.org/10.1016/j.cosust.2013.11.023.

Guest, J.R., Low, J., Tun, K., Wilson, B., Ng, C., Raingeard, D., Ulstrup, K.E., Tanzil, J.T.I., Todd, P.A., Toh, T.C., McDougald, D., Chou, L.M., Steinberg, P.D., 2016. Coral community response to bleaching on a highly disturbed reef. Sci. Rep. 6, 20717. http://dx.doi.org/10.1038/srep20717.

Hansen, J., Sato, M., Kharecha, P., Beerling, D., Masson-delmotte, V., Pagani, M., Raymo, M., Royer, D.L., Zachos, J.C., 2008. Target atmospheric CO 2: where should humanity aim? Open Atmos. Sciences 2, 217–231.

Hasler, H., Ott, J.A., 2008. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea. Mar. Pollut. Bull. 56, 1788–1794. http://dx.doi.org/10.1016/j.marpolbul.2008.06.002.

Hinderstein, L.M., Marr, J.C.A., Martinez, F.A., Dowgiallo, M.J., Puglise, K.A., Pyle, R.L., Zawada, D.G., Appeldoorn, R., 2010. Theme section on "mesophotic coral ecosystems: characterization, ecology, and management". Coral Reefs 29, 247–251. http://dx.doi.org/10.1007/s00338-010-0614-5.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742. http://dx.doi.org/10.1126/science.1152509.

Hoegh-Guldberg, O., Poloczanska, E.S., Skirving, W., Dove, S., 2017. Coral reef ecosystems under climate change and ocean acidification. Front. Mar. Sci. 4, 158. http://dx.doi.org/10.3389/fmars.2017.00158.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. Trends Ecol. Evol. 25, 633–642. http://dx.doi.org/10.1016/j.tree.2010.07.011.

Hughes, T.P., Kerry, J.T., Simpson, T., 2018a. Large-scale bleaching of corals on the great barrier reef. Ecology 99http://dx.doi.org/10.1002/ecy.2092. 501–501.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson, S.K., 2018b. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359, 80–83. http://dx.doi.org/10.1126/science.aan8048.

Iglesias-Prieto, R., Matta, J.L., Robins, W.A., Trench, R.K., 1992. Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proc. Natl. Acad. Sci. U. S. A. 89, 10302–10305.

IPCC, 2007. Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 996.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637. http://dx.doi.org/10.1126/science.1059199.

Jackson, J., Donovan, M., Cramer, K., Lam, V., 2014. Status and trends of caribbean coral reefs: 1970-2012. In: Global Coral Reef Monitoring Network. IUCN, Gland, Switzerland, pp. 304.

Johannes, R.E., 1975. Pollution and degradation of coral reef communities. In: Wood, E.J.F., Johannes, R.E. (Eds.), Tropical Marine Pollution. Elsevier Scientific, Oxford, pp. 1–181.

Kaczmarsky, L., 2006. Coral disease dynamics in the central Philippines. Dis. Aquat. Org. 69, 9–21. http://dx.doi.org/10.3354/dao069009.

Kahng, S.E., Grigg, R.W., 2005. Impact of an alien octocoral, Carijoa riisei, on black corals in Hawaii. Coral Reefs 24, 556–562. http://dx.doi.org/10.1007/s00338-005-0026-0.

Kahng, S.E., Garcia-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L., Toonen, R.J., 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29, 255–275. http://dx.doi.org/10.1007/s00338-010-0593-6.

Kahng, S., Copus, J., Wagner, D., 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Curr. Opin. Environ. Sustain. 7, 72–81. http://dx.doi.org/10.1016/j.cosust.2013.11.019.

Kelly, R.P., Foley, M.M., Fisher, W.S., Feely, R.A., Halpern, B.S., Waldbusser, G.G., 2011. Mitigating local causes of ocean acidification with existing laws. Science 332, 1036–1037.

Kirtman, B., Akintayo John Adedoyin, G.J.B., Bojariu, R., Camilloni, I., Doblas-Reyes, F., Fiore, A.M., Kimoto, M., Meehl, G., Prather, M., Sarr, A., Schär, C., Sutton, R., Geert Jan van Oldenborgh, G.V., Wang, H.-J., 2013. Near-term climate change: projections and predictability. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, A.J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, http://dx.doi.org/10.1017/CB09781107415324.

Kleypas, J.A., Langdon, C., 2006. Coral reefs and changing seawater chemistry. Coast. Estuar. Stud. 110, 61–73.

Kleypas, J.A., McMaus, J.W., Menez, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? Am. Zool. 39, 146–159. http://dx.doi.org/10.1093/icb/39.1.146.

Kroeker, K.J., Kordas, R.L., Crim, R.N., Singh, G.G., 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol. Lett. 13, 1419–1434. http://dx.doi.org/10.1111/j.1461-0248.2010.01518.x.

Ku, K., Chen, T., 2013. A conceptual process-based reference model for collaboratively managing recreational scuba diving in Kenting National Park. Mar. Pol. 39, 1–10. http://dx.doi.org/10.1016/j.marpol.2012.09.008.

Leão, Z.M.A.N., Kikuchi, R.K.P., Testa, V., 2003. Corals and coral reefs of Brazil. In: Cortés, J. (Ed.), Latin American Coral Reefs. Elsevier Science, Amsterdam, pp. 9–52. http://dx.doi.org/10.1016/B978-044451388-5/50003-5.

Leão, Z.M.A.N., Kikuchi, R.K.P., Ferreira, B.P., Neves, E.G., Sovierzoski, H.H., Oliveira, M.D.M., Maida, M., Correia, M.D., Jhonsson, R., 2016. Brazilian coral reefs in a period of global change: a synthesis. Braz. J. Oceanogr. 64, 97–116. http://dx.doi.org/10.1590/S1679-875920160916064sp2.

Loh, T., Mcmurray, S.E., Henkel, T.P., Vicente, J., Pawlik, J.R., 2015. Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. PeerJ 13, e901. http://dx.doi.org/10.7717/peerj.901.

Lough, J.M., 2012. Small change, big difference: sea surface temperature distributions for tropical coral reef ecosystems. J. Geophys. Res. Ocean 117, 1950–2011. http://dx.doi.org/10.1029/2012JC008199.

Lough, J.M., Oppen, M.J.H. Van, 2009. Introduction: coral bleaching - patterns, processes, causes and consequences. In: van Oppen, Madeleine J.H., Lough, Janice M. (Eds.), Coral Bleaching - Patterns, Processes, Causes and Consequences. Springer, pp. 1–6.

Loya, Y., Lubinevsky, H., Rosenfeld, M., Kramarsky-Winter, E., 2004. Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. Mar. Pollut. Bull. 49, 344–353. http://dx.doi.org/10.1016/j.marpolbul.2004.06.011.

Loya, Y., Eyal, G., Treibitz, T., Lesser, M.P., Appeldoorn, R., 2016. Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35, 1–9. http://dx.doi.org/10.1007/s00338-016-1410-7.

Marimuthu, N., Jerald Wilson, J., Vinithkumar, N.V., Kirubagaran, R., 2013. Coral reef recovery status in South Andaman Islands after the bleaching event 2010. J. Ocean Univ. China 12, 91–96. http://dx.doi.org/10.1007/s11802-013-2014-2.

McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu, I., J, B., Beger, M., Campbell, S.J., Darling, E.S., Eakin, C.M.,

Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddack, M.J., Selig, E.R., van Woesik, R., 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7, e42884. http://dx.doi.org/10.1371/journal.pone.0042884.

McLeod, E., Anthony, K.R.N., Andersson, A., Beeden, R., Golbuu, Y., Kleypas, J., Kroeker, K., Manzello, D., Salm, R.V., Schuttenberg, H., Smith, J.E., 2013. Preparing to manage coral reefs for ocean acidification: lessons from coral bleaching. Front. Ecol. Environ. 11, 20–27. http://dx.doi.org/10.1890/110240.

Menza, C., Kendall, M., Rogers, C., Miller, J., 2007. A deep reef in deep trouble. Continent. Shelf Res. 27, 2224–2230. http://dx.doi.org/10.1016/j.csr.2007.05.017.

Milazzo, M., Chemello, R., Badalamenti, F., Camarda, R., Riggio, S., 2002. The impact of human recreational activities in marine protected areas : what lessons should be learnt in the Mediterranean Sea? Mar. Ecol. 1, 280–290.

Morais, J., Santos, B.A., 2018. Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. Ecosphere. http://dx.doi.org/10.1002/ecs2.2281. (in press).

Mumby, P.J., 2016. Stratifying herbivore fisheries by habitat to avoid ecosystem over fishing of coral reefs. Fish Fish. 17, 266–278. http://dx.doi.org/10.1111/faf.12078.

Mumby, P.J., Hastings, A., Edwards, H.J., 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450, 98–101. http://dx.doi.org/10.1038/nature06252.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Slater, R.D., Totterdell, I.J., Weirig, M., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437, 681–686. http://dx.doi.org/10.1038/nature04095.

O'Gorman, K.D., 2009. Philosophical issues in tourism (aspects of tourism). Tourism Manag. 31, 293–294. http://dx.doi.org/10.1016/j.tourman.2009.04.007.

Palumbi, S.R., Barshis, D.J., Traylor-Knowles, N., Bay, R.A., 2014. Mechanisms of reef coral resistance to future climate change. Science 344, 895–898.

Pauly, D., 1988. Some definitions of overfishing relevant to coastal zone management in Southeast Asia. Trop. Coast. Area Manag. 3, 14–15.

Quéré, C.L., Raupach, M.R., Canadell, J.G., Marland, G., 2009. Trends in the sources and sinks of carbon dioxide. Nat. Geosci. 2, 831–836. http://dx.doi.org/10.1038/ngeo689.

Randall, J.E., 1998. Zoogeography of shore fishes of the Indo-Pacific region. Zool. Stud. 37, 227–268.

Rasher, D.B., Engel, S., Bonito, V., Fraser, G.J., Montoya, J.P., Hay, M.E., 2012. Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oceanography 169, 187–198. http://dx.doi.org/10.1007/s00442-011-2174-y.

Reopanichkul, P., Schlacher, T.A., Carter, R.W., Worachananant, S., 2009. Sewage impacts coral reefs at multiple levels of ecological organization. Mar. Pollut. Bull. 58, 1356–1362. http://dx.doi.org/10.1016/j.marpolbul.2009.04.024.

Richmond, R.H., 1993. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. Am. Zool. 33, 524–536.

Roche, H.R., Salvat, B.S., Ramade, F.R., 2011. Assessment of the pesticide pollution of coral reef communities from French Polynesia. Rev. d'Ecologie 66, 3–10.

Roche, R.C., Harvey, C.V., Harvey, J.J., Kavanagh, A.P., Mcdonald, M., John, V.R.S., 2016. Recreational diving impacts on coral reefs and the adoption of environmentally responsible practices within the scuba diving industry. Environ. Manag. 58, 107–116. http://dx.doi.org/10.1007/s00267-016-0696-0.

Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T., Kozyr, A., 2004. The oceanic sink for anthropogenic CO_2. Science 305, 367–372.

Sandin, S.A., Smith, J.E., Demartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the northern line islands. PLoS One 3, e1548. http://dx.doi.org/10.1371/journal.pone.0001548.

Sarkar, S., Ghosh, A.K., 2013. Coral bleaching a nemesis for the Andaman reefs: building an improved conservation paradigm. Ocean Coast Manag. 71, 153–162. http://dx.doi.org/10.1016/j.ocecoaman.2012.09.010.

Sasano, M., Imasato, M., Yamano, H., Oguma, H., 2016. Development of a regional coral observation method by a fluorescence imaging LIDAR installed in a towable buoy. Rem. Sens. 8, 48. http://dx.doi.org/10.3390/rs8010048.

Sassi, R., Francisca, C., Sassi, C., Gorlach-lira, K., Fitt, W.K., 2015. Pigmentation changes in *Siderastrea* spp. during bleaching events in the costal reefs of northeastern Brazil. Lat. Am. J. Aquat. Res. 43, 176–185. http://dx.doi.org/10.3856/vol43-issue1-fulltext-15.

Scopelitis, J., Andrefouet, S., Phinn, S., Chabanet, P., Naimc, O., Tourrand, C., Done, T., 2009. Changes of coral communities over 35 years: integrating in situ and remote-sensing data on Saint-Leu Reef. Estuar. Coast Shelf Sci. 84, 342–352. http://dx.doi.org/10.1016/j.ecss.2009.04.030.

Shlesinger, T., Grinblat, M., Rapuano, H., Amit, T., Loya, Y., 2017. Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. Ecology 12, 3218–3221. http://dx.doi.org/10.1002/ecy.2098.

Smith, L.W., Birkeland, C., 2007. Effects of intermittent flow and irradiance level on back reef *Porites* corals at elevated seawater temperatures. J. Exp. Mar. Biol. Ecol. 341, 282–294. http://dx.doi.org/10.1016/j.jembe.2006.10.053.

Sogin, E.M., Putnam, H.M., Anderson, P.E., Gates, R.D., 2016. Metabolomic signatures of increases in temperature and ocean acidification from the reef-building coral, *Pocillopora damicornis*. Metabolomics 12, 1–12. http://dx.doi.org/10.1007/s11306-016-0987-8.

Souter, D.W., Lindén, O., 2000. The health and future of coral reef systems. Ocean Coast Manag. 43, 657–688. http://dx.doi.org/10.1016/S0964-5691(00)00053-3.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and Shelf areas. Bioscience 57, 573–583. http://dx.doi.org/10.1641/B570707.

Stella, J.S., Munday, P.L., Jones, G.P., 2011. Effects of coral bleaching on the obligate coral-dwelling crab Trapezia cymodoce. Coral Reefs 30, 719–727. http://dx.doi.org/10.1007/s00338-011-0748-0.

Swain, T.D., DuBois, E., Gomes, A., Stoyneva, V.P., Radosevich, A.J., Henss, J., Wagner, M.E., Derbas, J., Grooms, H.W., Velazquez, E.M., Traub, J., Kennedy, B.J., Grigorescu, A.A., Westneat, M.W., Sanborn, K., Levine, S., Schick, M., Parsons, G., Biggs, B.C., Rogers, J.D., Backman, V., Marcelino, L.A., 2016. Skeletal light-scattering accelerates bleaching response in reef-building corals. BMC Ecol. 16, 10. http://dx.doi.org/10.1186/s12898-016-0061-4.

Thompson, A.A., Dolman, A.M., 2010. Coral bleaching: one disturbance too many for near-shore reefs of the Great Barrier Reef. Coral Reefs 29, 637–648. http://dx.doi.org/10.1007/s00338-009-0562-0.

Uyarra, M.C., Watkinson, A.R., Côté, I.M., 2009. Managing dive tourism for the sustainable use of coral reefs: validating diver perceptions of attractive site features. Environ. Manag. 43, 1–16. http://dx.doi.org/10.1007/s00267-008-9198-z.

Veron, J.E.N., Devantier, L.M., Turak, E., Green, A.L., Kininmonth, S., Stafford-Smith, M., Peterson, N., 2009. Delineating the coral triangle. Galaxea 11, 91–100. http://dx.doi.org/10.3755/galaxea.11.91.

Vogel, N., Meyer, F.W., Wild, C., Uthicke, S., 2015. Decreased light availability can amplify negative impacts of ocean acidification on calcifying coral reef organisms. Mar. Ecol. Prog. Ser. 521, 49–61. http://dx.doi.org/10.3354/meps11088.

West, K., Woesik, R. Van, 2001. Spatial and temporal variance of river discharge on Okinawa (Japan): inferring the temporal impact on adjacent coral reefs. Mar. Pollut. Bull. 42, 864–872. http://dx.doi.org/10.1016/S0025-326X(01)00040-6.

Wild, C., Hoegh-guldberg, O., Naumann, M.S., Colombo-pallotta, M.F., Ateweberhan, M., Fitt, W.K., Iglesias-prieto, R., Palmer, C., Bythell, J.C., Ortiz, J., Loya, Y., Woesik, R. Van, 2011. Climate change impedes scleractinian corals as primary reef ecosystem engineers. Mar. Freshw. Res. 62, 205–215.

Wilkinson, C., 2008. Status of coral reefs of the world: 2008. Status Coral Reefs World 2008, 5–19.

Williams, C., 1997. Combatting marine pollution from land-based activities: Australian initiatives. Ocean Coast Manag. 33, 87–112.

Wynn, R.B., Huvenne, V.A.I., Le Bas, T.P., Murton, B.J., Connelly, D.P., Bett, B.J., Ruhl, H.A., Morris, K.J., Peakall, J., Parsons, D.R., Sumner, E.J., Darby, S.E., Dorrell, R.M., Hunt, J.E., 2014. Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. Mar. Geol. 352, 451–468. http://dx.doi.org/10.1016/j.margeo.2014.03.012.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., Mcminds, R., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. 7, 11833. http://dx.doi.org/10.1038/ncomms11833.